The Island Test for Cumulative Culture in Paleolithic Cultures

Tennie, Claudio; Braun, David; Premo, Luke ; McPherron, Shannon

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Claudio Tennie, Max Planck Institute for Evolutionary Anthropology, Deutscher Platz 6, 04103 Leipzig, Germany & School of Psychology, University of Birmingham, Birmingham, B15 2TT, UK.

Correspondence to: c.tennie@gmail.com.

David R. Braun, University of Cape Town, South Africa and Center for the Advanced Study of Hominin Paleobiology, Department of anthropology, George Washington university, 2210 G Street NW, Washington DC 20052

Luke S. Premo, Department of Anthropology, Washington State University, Pullman, WA 99164-4910 and Max Planck Institute for Evolutionary Anthropology, Deutscher Platz 6, 04103 Leipzig, Germany.

Shannon P. McPherron, Max Planck Institute for Evolutionary Anthropology, Deutscher Platz 6, 04103 Leipzig, Germany.

Abstract

Early Stone Age artifacts have long been assumed to reflect the material record of communities whose members possessed the ability to transmit ideas, behaviors, and technologies from individual to individual though high-fidelity transmission (i.e., involving teaching and/or imitation), much like humans do today. Recent experimental work has highlighted marked differences between great apes and modern humans in the capacity and/or motivation for some forms of cultural transmission. In particular, high-fidelity mechanisms of social learning, which are thought to underlie the capacity for cumulative culture, appear to be enhanced in - if not unique to - humans. Taken as a group, these experiments suggest it is plausible that a combination of genetic, environmental, and social factors that do not include high-fidelity social learning mediate the ”cultures” described for great ape populations to date. It may be that, while the distribution of great ape behavioral variation in time and space is likely affected by low-fidelity social learning (which is widespread in the animal kingdom) the observed variants were invented (i.e., learned) independently by each individual rather than copied from other individuals. Behaviors that do not require high-fidelity transmission between individuals in order to increase in frequency in a population lie within the so-called “zone of latent solutions.” Here, we begin to grapple with the hypothesis that much of the Early Stone Age archaeological record may reflect deeply “canalized” behaviors of hominin toolmakers—those that reside in each individual’s zone of latent solutions—rather than behaviors that necessarily require high-fidelity transmission between individuals. We explore this possibility while eschewing the simplistic notion that variation in stone tool shape, for example, is entirely determined by the genetic variation found in the toolmakers. Instead, we suggest that the variation observed in Early Stone Age artefacts may simply reflect a heavier reliance on behaviors that reside within the zone of latent solutions than on behaviors that make use of high-fidelity social learning. We discuss a thought experiment, called the Island Test, which may be useful for distinguishing hominin behaviours that require high-fidelity transmission from behaviours that do not. We conclude that the Early Stone Age archaeological record is consistent with the possibility that latent solutions explain the behavioral variation inferred from available material culture. Furthermore we explore reasons why the assumption of high fidelity transmission associated with Paleolithic industries is difficult to support.

"Most scholars assume that the skills necessary to manufacture Acheulean tools were transmitted culturally in the same way that stone tool traditions are transmitted among living foragers. However, this assumption is hard to reconcile with either theory or data. […] perhaps we need to entertain the hypothesis that Acheulean bifaces were innately constrained rather than wholly cultural and that their temporal stability stemmed from some component of genetically transmitted psychology."

Richerson and Boyd 2005: p. 142

Introduction

In recent years it has become apparent that trying to understand modern human evolution without understanding some features of cultural evolution is untenable (Brown et al. 2011), for cultural evolution is inextricably linked to biological evolution in humans (Laland et al. 2010). These points further justify the use of gene-culture co-evolution, or dual inheritance, theory (Boyd and Richerson 1985; Richerson and Boyd 2005; Richerson et al. 2010) and human niche construction, or triple inheritance (genes, culture, and ecology), theory (Odling-Smee et al. 2003; Rendell et al. 2011). While these perspectives have undoubtedly opened new avenues for understanding human evolution, applications to earlier hominins tend to paint with a broad brush—as Richerson and Boyd acknowledge in the quote above—treating their subjects as more or less equivalent to modern humans with regard to the capacity for cultural transmission.

While numerous studies show that "tool use cultures" may be present in some great ape species (Whiten et al. 1999; Byrne 2002; Carvalho et al. 2008; Schöning et al. 2008; Marshall-Pescini and Whiten 2008; McGrew 1998; Haslam et al. 2009), suggesting that humans are not the only ones with culture writ large, it remains that modern human culture may be unique in important ways (Tomasello 1999; Hill et al. 2009). In particular, human cultural change is associated with a ratcheting effect, referred to as cumulative cultural evolution (Tomasello 1999), that may prove to be a unique feature of the hominin lineage (Tennie et al. 2009, though see Pradhan et al. 2012 for an alternative view) even if we do not yet know when it evolved. Although the list of cognitive ingredients thought to be sufficient for cumulative culture remains a source of debate, many agree that cumulative culture (at least the human version) is not possible without high-fidelity social learning mechanisms, such as teaching and imitation (Tomasello 1999). This is one reason why those searching for cumulative culture in non-humans have been interested in identifying examples of imitation and teaching in ape societies. While some argue for the presence of imitation in chimpanzees (De Waal 2001; Whiten et al. 2009a), others remain skeptical (Tennie et al. 2012) or insist that if chimpanzees do indeed imitate, they do so less regularly and with less fidelity than humans (Tennie et al. 2009; Whiten et al. 2009a). Currently there is no credible evidence to support evidence of active teaching in chimpanzees (Tennie et al. 2009).

Although there is still some debate on the presence of high-fidelity transmission in apes, it appears that chimpanzees do have some low-fidelity social learning abilities, as shown convincingly in laboratory settings (Whiten et al. 2009a). In addition, some behavioral patterns are different among populations of closely related chimpanzees who live in similar environmental contexts, suggesting that the behavioral variation is not well explained by a purely genetic or environmentally deterministic explanation (Gruber et al. 2009; Luncz et. al. 2012). To paleoanthropologists on the outside looking in, the mounting evidence gathered from ape societies provides a unique view of what cultural variation looks like in the absence of the type of pervasive high-fidelity cultural transmission that characterizes humans today.

Research conducted by one of us (CT) on the mechanisms that drive cultural variation in ape societies (Tennie et al. 2009, 2010; Tennie and Hedwig 2009) identifies two important factors. First, many primate behaviors that are considered "cultural" in naturalistic settings can be (re)invented by a single naïve individual that did not have access to an experienced model, or teacher (Tennie et al. 2008; Visalberghi 1987; Menzel et al. submitted). The particular *form* that any such behavior takes thus appears to result from a complex and admittedly opaque interaction between the environmental conditions and genetic predispositions of the individual rather than from high-fidelity transmission between individuals. Second, low-fidelity mechanisms of social learning, including stimulus enhancement (Whiten and Ham, 1992), can influence how often, by whom, where, to what and when such a behavior is expressed. Thus, low-fidelity social learning plays a role mainly in influencing the temporal and spatial distribution of variation in individually learned behaviors (Tennie et al. 2009).

Together these two factors constitute the “zone of latent solutions” hypothesis (hereafter ZLS).[1] Behaviors or variants that do not require high-fidelity social learning in order to increase in frequency in a population lie within a species’ ZLS. Thus, behaviors that reside in the ZLS are not indicative of cumulative culture. A ZLS-based explanation provides a valid alternative for interpreting the currently available data concerning chimpanzee culture (both from field observations and lab experiments; Tennie et al. 2009). One of the reasons for introducing the ZLS here is that we think the concept might also provide a useful framework for studying and ultimately interpreting the variation in Early Stone Age archaeological assemblages.

Galef (2001) has claimed that unless imitation has actually been shown to underlie the spread of a behaviour, that behaviour should be considered a tradition rather than culture. We recognize that there should be some distinction between animal traditions and modern human cultures. However, here we follow Whiten and Van Schaik (2007) in making a distinction instead between culture that does not require imitation (i.e., ‘a distinctive behavior pattern shared by two or more individuals in a social unit,

[1] The term “solutions” is used because social learning experiments often focus on physical problems to solve. But the hypothesis may also be called more broadly “zone of latent behavior,” as indeed the theory also entails social behaviors such as “hand-clasp grooming” (Tennie et al. 2009) that may not be best described as “solutions.” Nevertheless, here we stick to the original term so as not to introduce ever more terms.

which persists over time and that new practitioners acquire in part through socially aided learning… ' (Fragaszy and Perry 2003) to which we would add: "…usually with the exception of imitation") and cumulative culture that accumulates through imitation or teaching (Tennie et al. 2009). This distinction seems heuristically pragmatic because culture is the term most often used in descriptions of great ape behavior (e.g., Whiten 2000). Following this definition, culture can be sustained by several social learning mechanisms and it does not necessarily require imitation. Cumulative culture is distinctive in that it requires the underlying mechanism of high fidelity transmission (imitation or teaching; Tomasello 1999).

To date, primatologists have spent far more time studying cultures that do not exhibit pervasive high-fidelity social learning (McGrew 1998; Whiten et al. 1999; Matsuzawa et al. 2001; Biro et al. 2003; Horner and Whiten 2005; Lycett et al. 2007; Schöning et al. 2008; Whiten et al. 2009a) than have Paleolithic archaeologists, but maybe this should change. We might begin by asking whether the Early Stone Age archaeological record is consistent with the predictions of an explanation that places the behaviors responsible for the manufacture, use, and discard of stone tools within the ZLS of the hominin toolmakers. Considering the many similarities between humans and their closest living relatives today, we can expect that some basic—though not yet cumulative—cultural patterns existed deep in the past (and maybe that variation looked similar to what we see within and between ape societies today). However, at the point in hominin evolution when high-fidelity social learning became the rule rather than the exception, culture became cumulative. Identifying when this occurred and explaining why it happened when it did, strike us as extremely important yet neglected paleoanthropological research questions. Given that technology and associated selective advantages are one of the most pervasive features of hominin adaptation for at least the last 60ka, it seems imperative that paleoanthropologists address the mechanisms of how it arises and spreads.

The assumption that early stone tools represent cumulative culture is commonly made (Gamble 2005; Shipton 2010), if not explicitly stated (although see the critique in Richerson and Boyd 2005; Acerbi et al. 2011). Models that treat early stone tool technology as representative of the toolmakers' ability to transfer the information needed to manufacture the implements through high- (or at least, medium-) fidelity copying also view high-fidelity cultural transmission as having been a feature of the hominins for at least 2.5 million years (Whiten et al. 2011). In a bit of a departure, McNabb et al. (2004) suggest that while patterns of variation in large stone cutting tools from southern Africa may imply that Acheulean tools were mimetic constructs (and that their main "idea" needed to be transmitted rather than learned individually), they argue against the notion that what was being culturally transmitted was a detailed mental template.

Here, we entertain an alternative hypothesis that suggests that much of the Early Stone Age cultural material record may be explained by latent solutions rather than by behaviors that require high-fidelity forms of social learning, such as imitation or teaching. This perspective holds that the flint-knapping techniques for making Oldowan and even Acheulean tools fit squarely within the ZLS of Early Stone Age hominins. This explanation also assumes that, although the technological know-how did not require high-fidelity transmission, low-fidelity social learning such as stimulus enhancement and product emulation (sensu Tennie et al. 2009) could have played a role in the spatial and temporal distributions of the otherwise independently invented (i.e., individually learned) toolmaking behaviors as well as the archaeological assemblages those behaviors left behind.

If the appearance of simple flaked stone implements at 2.5 million years ago is not sufficient to signal the presence of cumulative culture and the high-fidelity social learning mechanisms that underlie it, then what is? When using the Paleolithic archaeological record to address this question we must be careful to consider whether other mechanisms might have been responsible for the spatial and temporal variation in culture material before settling on cultural transmission as the best working hypothesis. A more conservative approach, given the apparent rarity (or quite possibly, absence) of cumulative culture in apes, would be to treat a ZLS explanation as the default for Early Stone Age hominins until it can be shown that the archaeological data demonstrate otherwise.

The Archaeological Record of Oldowan and Acheulean

The Oldowan is well dated in sites that are at least as old as 2.5 Ma in the Gona region of Ethiopia (Semaw et al. 1997; Semaw 2000). However, this is the only locality where sites of this antiquity are known. By 2.3 Ma localities elsewhere in Ethiopia and in various parts of Kenya are known (Kimbel et al. 1996, Roche et al. 1999). By 1.8 Ma much of the African continent appears to be inhabited by tool using hominins and shortly after this we begin to see their appearance throughout the Old World (Kuman and Clarke 2000; de Lumley et al. 2005; Sahnouni et al. 2009). Although there are a few that would suggest linear patterns of increasing complexity throughout the Oldowan (Carbonell et al. 2006), the dominant and constant feature of the Oldowan is pebble tools (or “cores”) that have been knapped to produce flakes with sharp edges. Experimental studies have shown that most of these cores are not useful for many of the activities we assume early hominins were engaged in (e.g., butchery, woodworking (Toth 1987)). Importantly, the most prominent feature of the Oldowan is that there does not appear to be variation in stone tool technologies at a given time that cannot be explained by environmental factors [although see Whiten et al. (2009b) for possible explanatory scenarios], and time transgressive variation does not display patterning that differs from variation among assemblages that have been dated to similar time periods. By some measures, the degree of Oldowan behavioral variation revealed by stone tools appears even less patterned than that described for chimpanzees (Lycett et al. 2007).

Hominins likely invested substantial energy in the development and maintenance of stone tool kits (Stout et al. 2005; Braun et al. 2008; Braun et al. 2009), and the production of these artifacts was likely bound by certain rules of manufacture (Delagnes and Roche 2005). However, whether or not any of these rules benefitted from or, more to the point at hand, *required* high-fidelity transmission processes remains unknown. We find it difficult to identify characteristics of the Oldowan record that preclude the possibility that multiple bouts of individual learning (i.e. naïve individuals applying largely biologically based skills) were responsible for these artefacts. Oldowan tool manufacture and use may have been deeply canalized behaviors that resided within the ZLS of Early Stone Age hominins. Here, just like in the case of living chimpanzees, it is also possible that some low-fidelity social learning mechanisms facilitated the distribution and frequency of behaviors. Such social learning most likely increased the likelihood that certain locations would become foci of stone artifact production behavior. Studies of Oldowan behavior have already documented that the presence of raw material and resources that require tool use will result in archaeological assemblages that are significantly larger than assemblages found in areas with reduced availability of stone or reduced requirement for stone tools (Braun and Harris 2009). Although the population size of ancient hominin groups is poorly understood, increases in census size could have facilitated the distribution of this behavior as this could have increased the probability of the expression of latent solution behaviours (Tennie et al. 2009).

While a latent solutions explanation may account for the Oldowan, handaxes, the hallmark of the Acheulean, may (at first) appear to be a qualitatively different case. The earliest handaxes occur between ~1.8 (Lepre et al. 2011) and 1.4 (Asfaw et al. 1992) Ma and continue in a generally similar format for over a million years. It is generally understood that the production quality of handaxes increases over time (i.e. tools become more refined, more regular, more symmetrical), although a systematic time transgressive study of this has yet to be conducted. This change—if real—could be considered to be a cumulative expansion of the previous tool production techniques. As such, it has been suggested that this may represent an ancient reflection of the ratcheting effect of human culture (Stout 2011). However, demonstrating this point quantitatively has been complicated by the high level of variability that exists at any one time, the number of variables that may influence final form, and the paucity of well dated assemblages. Further, the amount of time covered by the Acheulean means that biological explanations (e.g., physiological changes that improved motor skills; or increased working memory, see Haidle 2010) could account for some improvements in handaxes through time. It is also worth noting that handaxes are found throughout large portions of the Old World and were very likely made by *multiple* hominin species.

Where they principally differ from the preceding Oldowan, however, is in the notion that handaxes are consciously shaped to a particular form both by the controlled removal of shaping flakes and, in some cases, by the intentional preparation of large initial forms particularly suited to handaxe (and cleaver) production (Sharon 2007). The amount of effort, in terms of either the number of shaping flakes removed or the steps involved in preparing the blank, varies across the distribution of the Acheulean in both time and space, resulting in a positive assortment of particular forms or techniques. This apparent complexity has led some to suggest that handaxes must represent a true cultural advance over earlier stone tools, and some have gone so far as to suggest that extremely high levels of conformist biased cultural transmission were responsible for keeping handaxe form in check (Whiten et al. 2003; Lycett and Gowlett 2008; Shipton 2010). The clear implication of these studies is that handaxe form fully *depended* on high-fidelity cultural transmission whether or not this term is explicitly mentioned (Shipton 2010).

If the assumption that the form of handaxes was dependent on a behavior that required high-fidelity cultural transmission is correct, then one might reasonably expect patterns of cultural adaptation associated with handaxes to reflect this. The question is whether the signature of cultural transmission is evident in the archaeological record? To answer this question we need to think more about what that signature would look like and how we could assess our own confidence in recognizing it in archaeological data.

One challenge to answering these questions concerns the significance of both the similarity and the variation in handaxes. On the one hand, despite their dramatic geographic distribution, the remarkable similarity of large cutting tools distinguishes the Acheulean industry from subsequent lithic industries. A pattern of ubiquity across landscapes, through long periods of time, and across multiple species suggests an explanation within the domain of latent solutions. Yet, on the other hand, some variation in handaxes is observed. Mostly the focus here has been on handaxe shape and its significance, but aside from shape variation at the continental scale (Wynn and Tierson 1990; McPherron 2000; Lycett 2008; Lycett and Gowlett 2008) it has not been demonstrated that shape varies in patterned ways that are not largely accountable for by raw material variability and the intensity of bifacial reduction (e.g., the debate over the significance of variability in the British handaxe assemblages, see White 1998; McPherron 2007). Shape variability at a continental scale may be driven by similar ecological factors, as there are no independent lines of evidence to suggest the presence of continental scale cultural norms during this period. Another aspect of variability is in the techniques used to produce large flakes on which handaxes are sometimes made. Some have suggested that the type and form of raw materials that were used to make Acheulean tools reflects distinct selection biases on the part of individuals, decisions that have consequences for the shape of the handaxes fashioned on those raw materials (Sharon 2007, 2008; Shipton et al. 2009; Goren-Inbar 2011). The question is whether this variability demonstrates high-fidelity cultural transmission, and we believe that the answer is: not necessarily. Low-level learning mechanisms such as stimulus enhancement would result in similar patterns (see Tennie et al. 2009).

Richerson and Boyd (2005:142) outline the crux of this argument: "How could cultural transmission alone, particularly if based on a relatively primitive imitative capacity, preserve such a neat, formal-looking tool as a Acheulean hand-axe over half the Old World for a million years?" Or, phrased differently, could an artifact form as apparently complex as an Acheulean handaxe persist for so long in such a recognizable form over such a large geographic area in the absence of high-fidelity cultural transmission? We appreciate the fact that suggesting that the latter can be answered in the affirmative may be hard to digest at first (it sure was for some of us). We are in no way suggesting that there is a gene that "codes for" a certain type of handaxe production, yet we think it can be productive to consider whether the behavior(s) responsible for Oldowan core or Acheulean handaxe manufacture, use, and discard belongs within the ZLS of Early Stone Age hominins. Principally this is important because it forces one to be explicit about the characteristics of the behaviors that would necessitate an explanation that invokes high-fidelity cultural transmission. It is difficult to formulate useful tests of the empirical record until these assumptions have been made explicit and their qualities have been discussed and assessed by other experts.

The Island Test for Cumulative Culture

So, what is the likelihood of handaxes or any other Early Stone Age stone tool technology being the result of latent solutions? The term "latent solution" refers to a behavior that lies "dormant" or "latent" in an individual until triggered by a particular set of social or environmental cues and sufficient motivation on the part of the learner. Indeed the pattern of occurrence in naïve individuals who had no access to experienced models was the very mark of latent solutions that led to the initial description of the ZLS (see Tennie et al. 2009). Thus, one way to address the question above is to identify behaviors that could be exhibited by a previously naïve individual in the absence of any other cultural models. This is captured by a thought experiment that we refer to as the “Island Test” (based on a hypothetical island scenario presented first by Tomasello (1999)). Consider a scenario in which a child born to Early Stone Age hominin toolmakers is separated at birth and “magically” raised alone on an island that provides all of the raw material and motivation needed to produce Oldowan or Acheulean stone implements. Would this solitary hominin, stripped of the benefit of observing, let alone being taught by, another toolmaker, produce, use, and discard artefacts that are indistinguishable from those we observe in the Early Stone Age archaeological record? If the behavior responsible for that kind of stone tool manufacture can be independently invented (i.e., learned, not copied) by a solitary individual and, thus, does not require high-fidelity cultural transmission, then it fails the Island Test for cumulative culture. We speculate that much of the early Paleolithic archaeological record may be composed of implements that resulted from behaviors that would fail such a “test.” If we are correct in that assertion, then those behaviors reside within the zone of latent solutions of Early Stone Age hominins.

Our proposition may seem overly conservative at first. Considering the difficulty that most naïve (i.e., beginner) human flintknappers have today in learning how to produce a simple flake tool (e.g. Nonaka et al. 2010), can we safely assume that the behaviors responsible for creating what appear to us to be complex forms, such as the Acheulean handaxe, do not require the ratcheting effect of cumulative culture? In our view, the latent solutions explanation serves as a useful null model for early hominin behavior, which in turn should be viewed in the larger context of animal behavior (all hominins are animals, after all). Perhaps a ZLS explanation for early stone tool technologies appears less extreme if we consider Oldowan and Acheulean stone tools as similar to other complex “artefacts” such as beaver dams[2], weaver bird nests, and spider webs—structures resulting from behaviors that are not regarded as requiring high-fidelity cultural transmission. Would dam building in beavers pass the Island Test? If we placed a single, normally developed, yet dam-naïve beaver on an island with the motivation and material to produce a dam (including water) would it eventually build a dam? We think the intuitive answer is yes, it would (though of course, this remains to be seen). Also, it has already been shown that other seemingly complex behaviors do not require cultural transmission [e.g., naïve woodpecker finches can also make use of tools (Tebbich et al. 2001); see examples for great apes in (Tennie et al. 2009)].

A latent solutions explanation only rules out high-fidelity social learning mechanisms. Considering the prevalence of low-fidelity social learning in species ranging from stickleback fish to bats, it is almost certain that many behaviors exhibited by hominins included at least some aspect of low-fidelity social learning (Laland et al. 2010). Indeed, it is worth investigating to what extent stimulus enhancement together with emulation learning and other low-fidelity social learning mechanisms (Laland and Hoppitt 2003, Tennie et al. 2009) might explain the low level of variation observed in Early Stone Age culture material. For example, a ZLS explanation in which low-fidelity social learning mechanisms can be

[2] One might object that it may transpire that beaver dams only look complex but may be based on simple iterative wood-placing techniques. The question of complexity in behavior is however a tricky one – and likely relative to the species in question. All that we suggest here that complexity alone cannot be solid ground for the inference of cumulative culture (Tennie & Hedwig 2009).

considered seems to fit the data as well as recently proposed demographic explanations of Acheulean geographic variation (Lycett and von Cramon-Taubadel 2008; Lycett and Norton 2010). Furthermore it does this without assuming modern human abilities of high-fidelity cultural transmission on Middle Pleistocene hominins.

Obviously, for the case of extinct hominin behaviors, the Island Test can never actually serve as a "test." However, the vagaries of prehistory may have resulted in conditions that approximate key aspects of the thought experiment. For example, as mentioned earlier, handaxes appear throughout the Old World beginning by the Middle Pleistocene but are conspicuously absent for much of the Pleistocene record in South East Asia. Lycett and Norton (2010) suggest this is the result of a decrease in population size such that the collective cultural store of knowledge was insufficient to keep Acheulean technology in the behavioral repertoire of hominins in East Asia. However, how can we explain the reappearance of the very same stone tool forms when people move back into the area or, in the case of Lycett and Norton's argument, when effective population sizes rebound? Yamei and colleagues (2000) suggest the presence of Acheulean tools in the Bose Basin is the result of the appearance of suitable raw materials in this region at this time. Thus, the reappearance of similar tool forms in the Bose Basin may be the result of the reappearance of the ZLS conditions that led to the behavior responsible for Acheulean handaxe production. Using estimates of population size through time in this region, it may be possible to assess which of these alternative hypotheses is better supported by the archaeological data. At any rate, the ZLS approach explicitly allows for a behavior to at times disappear and subsequently reappear in an identical form when the ecological setting that brought about the initial appearance of the behavior (in this case, suitable raw material – but there may be other reasons in different situations) resurfaces.

Zones of latent solutions: Archaeological expectations and complications

It is unfortunate that the Island Test ultimately does not provide much of a repeatable test for the case of Early Stone Age hominin behavior. Obviously, the thought experiment alone cannot "prove" that any Oldowan or Acheulean behavior was or was not a latent solution, nor is that the goal of this paper. But the Island Test does provide a heuristic device that can be used to improve our ideas about what kinds of archaeological signals we would expect latent solutions and culturally transmitted behaviors to exhibit in an assemblage of Paleolithic stone tools and debitage. Here, we begin to outline some of the archaeological expectations of a latent solution explanation. Our expectations cover three major components of variation in artefact form: geographic variation, temporal variation (the pace of change in form), and the reappearance of old, recognizable forms. We note that some expectations are not exclusive to a ZLS explanation. In addition, we briefly identify some reasons for caution when relying on the variation observed in stone tool technologies to discern latent solutions from cumulative cultural solutions.

Geographic variation. There is debate over whether geographic variants can be identified within the Acheulean (Wynn and Tierson 1990; Shipton and Petraglia 2010). Studies that suggest the presence of geographic variation (Wynn and Tierson 1990) have not gone without critics (McPherron 2000). Here, we are interested in identifying what we would expect to see in terms of geographic variation in stone tool assemblages under the assumption that they are individually learned and only indirectly influenced by low-level social learning mechanisms vs. the assumption that they are – and have to be – directly transmitted between individuals via high-fidelity social learning.

If ZLS behaviors were responsible for Early Stone Age tool manufacture and use, we would expect geographic variation in tool form (within a given species) to be explained by the combined effects of geographic variation in environmental conditions and low-level social learning mechanisms on raw material choice and possibly even core choice. This follows from the notion that the behavior an individual exhibits is influenced by both its psychology as well as its ecological and (low-level) social cues. Without independent measures of hominin psychology or of the particular low-level social cues involved, however, it may remain difficult to directly assess how much of the variation in the archaeological record is explained by the ZLS approach.

High-fidelity cultural transmission often results in striking geographic variation in tool forms. As Boyd and colleagues have shown, conformist biased cultural transmission can have the effect of increasing between-group differences even if there is migration between them (Boyd and Richerson 1985; Henrich and Boyd 1998; Richerson and Boyd 2005). In theory, conformist biased transmission can also have the effect of reducing within-group diversity to levels that may be similar to those predicted for a ZLS behaviour. In addition, if there is very little migration of individuals and/or ideas between geographically or culturally isolated groups, then one may expect between-group variation to arise from even unbiased cultural transmission (or "random copying"). However, unbiased cultural transmission will yield greater within-group variation than conformist biased transmission and, more importantly, possibly greater within-group variation than predicted by a latent solution. On the flip side, there are demographic conditions (such as frequent local extinction and repopulation events: Premo and Kuhn 2010; Premo 2012) that can reduce the amount of geographic variation observed between regions in a structured population of high-fidelity social learners.

It would appear that we do not yet have a good idea of what kind(s) of archaeological signal(s) in spatial variation in stone tool form would distinguish behaviors that do not require high-fidelity social learning from those that do. Spatially explicit computational modeling might provide the kind of heuristic tool needed to aid us in improving our expectations of the empirical record.

Temporal variation. How fast would we expect the form of an artefact to change through time in the absence of high-fidelity transmission? At first, it would seem that there is no simple answer to this question because the rate of change in a behavior that lies with the ZLS is contingent upon changes in the environment, low-level social learning mechanisms, and the psychology and physiology of the species of interest. While it may be possible in some cases to quantify the extent to which changes in artefact form correlate with changes in climate, this is a crude tool, at best.

Instead, it might be better to identify rates of change that we would *not expect* to see in the archaeological record if the behaviors responsible for stone tool manufacture were indeed latent solutions. For cases that involve cultural transmission, a baseline rate of change (between upper and lower bounds imposed by mechanical constraints of the implement) can be estimated by taking into consideration the size and rate of copying mistakes caused by perception error. Kempe et al. (2012)

analyze data collected from 2601 handaxes at 21 sites with a range of over one million years and show that handaxe form features actually changed more *slowly* than expected under the assumption that the form was passed via high-fidelity cultural transmission (which is subject to such perception error).

In the presence of cultural transmission, processes that affect the effective size of the population of social learners can also affect the rate of change. For example, *biased* forms of cultural transmission (which decrease the effective population size by reducing either the number of models a naïve individual can potentially learn from or the number of traits that a naïve individual can adopt) may speed up or slow down the rate of change observed in an assemblage. Demographic factors can also affect rates of change, even after holding copying error rate constant (e.g., Premo and Kuhn 2010). These complications are worth keeping in mind because the rate of change will have serious consequences for measures of diversity within and between spatially or temporally separated archaeological assemblages. In cases where biased forms of cultural transmission and demographic effects can be ruled out as the cause of low variation and slow rates of change in the material record, a ZLS explanation may provide the most parsimonious explanation precisely because it does not assume high-fidelity cultural transmission of traits in the first place – while it does predict slow change.

The reappearance of old forms. Another expectation of the latent solutions approach is that certain behaviors may disappear at times and subsequently reappear (in the identical form) if the environmental, cognitive, motivational and social conditions that helped to trigger the initial appearance return. Certainly the reappearance of Acheulean tools in the Bose Basin (Yamei et al. 200), for example, suggests the possibility that the identical forms were re-invented many generations after they had disappeared[3]. Clearly, in the case of "sophisticated" cumulative cultural technologies, like those we take for granted today, we would not expect the form of the "artefact" (say, a computer) to be similar to the form that disappeared hundreds of generations earlier simply because the large number of cumulative innovations required would allow for many deviations the second time around. While we would not expect the form of a tool that required high-fidelity transmission to be identical to the form that disappeared from the record earlier, this is precisely the expectation if the tool form resulted from a ZLS behaviour. Given the reappearance of the same combination of ecological, cognitive, motivational and social conditions responsible for the earlier appearance, we would expect to see a similar form. Having said that, in the case of a far less sophisticated cumulative cultural technology, in which the identical form can be recovered after the accumulation of just one or two innovations, it may be more difficult to discern a latent solution from one that requires cultural transmission in assemblages characterized by low temporal resolution. Given the apparent simplicity of Oldowan stone tools and the fact that many of the assemblages from this period conflate hundreds if not tens of thousands of years of time, distinguishing between the two alternatives may prove difficult in Oldowan assemblages.

[3] Also worth mentioning again in this context is that the manufacture of stone tools that look similar by different species is compatible with a ZLS explanation, which does not require further assumptions (i.e. high-fidelity social learning – and thus high tolerance – between different species).

It is most certainly not by design that stone tools comprise a very large proportion of all of the culture material recovered from the Oldowan and Acheulean. Previous research has identified the overriding importance of certain parameters that seem to guide all Acheulean tool production [e.g. correlation between elongation and any measure of size on almost all studied assemblages of handaxes; (McPherron 1999)]. Here, the relationship between major size-related variables suggests that there are very few ways to make a handaxe. Thus, the convergence on a similar shape (or in other terms, the movement to a strong basin of attraction among all possible implement shapes) may actually not be all that surprising (Stout 2011). A related concern is that the tempo of material culture change need not be at the same rate. If stone tool technology was one of the more conservative aspects of Early Stone Age hominin life (due to conformist biased transmission, for example) or if some tool forms are highly convergent, then they may provide a biased picture of cultural variation that leads us to the wrong conclusion about whether Early Stone Age hominins were capable of transmitting information through high-fidelity social learning. At the very least, is seems worth acknowledging that the simple fact that stone tools are what we have to study from these early periods does not mean they are the best (or maybe even a suitable) source of data to address all of the questions we wish to answer.

It is important to be pragmatic and rigorous in testing these alternative hypotheses against the Paleolithic material record. Equifinality among alternatives does not invalidate either the ZLS or high fidelity cultural transmission explanations a priori, but it is likely to complicate the task of creating tests with enough power to discern the signal of latent solutions from that of a behavior that requires high-fidelity transmission. However, if we are to determine the basic mechanism of cultural change in the past, these tests are necessary. Given our brief discussion of the archaeological expectations associated with low-fidelity and high-fidelity social learning mechanisms, it would appear that a ZLS account does a better job than those that assume high-fidelity cultural transmission of explaining some of the more vexing characteristics of the Early Stone Age stone tool data.

Conclusion

Here we have discussed the ZLS concept as a viable alternative explanation for patterns of variation in the Early Stone Age archaeological record. We submit that Early Stone Age tool technologies can plausibly be explained by behaviors that fall within their various hominin makers' "zone of latent solutions." One of the distinguishing characteristics of the ZLS explanation is that it does not require high-fidelity social learning mechanisms on the part of Oldowan and Acheulean toolmakers. More work is needed to test the validity of our claim, and we hope that this paper provides the impetus for that research.

The majority of evidence available to date suggests that cumulative culture—and, even more fundamentally, the high-fidelity mechanisms of social learning (including teaching) that make it possible—evolved in the hominin lineage sometime between the chimpanzee-human split and the late Pleistocene, when the record shows clear examples of rapidly changing geographically delineated "cultures" throughout the Old World. Important questions concerning exactly when, how, and why cumulative culture arose in hominins have remained largely unaddressed. The good news is that a number of recent studies attest to the fact that this is changing.

Stout and colleagues (Stout et al. 2010) evaluate the variation in stone tool form from a horizon in the Gona (Ethiopia) sequence in search of cumulative culture. Although they note interesting patterns of variation in the assemblage, they were (in our view) unable to definitively exclude the possibility that the observed variation resulted from behaviors that did not require high-fidelity cultural transmission. At the opposite end of the Paleolithic, the stylistic motifs that decorate ostrich eggshell from Diepkloof Rock Shelter (Western Cape of South Africa) provide better candidates for early examples of cumulative culture (Texier et al. 2010). Texier and colleagues document variation over a period of possibly as little as 5000 years in designs on ~60,000 year old ostrich eggshells. Because these motifs were unlikely to have been affected by differences in subsistence they probably represent evidence of stylistic change through time. In other words, it appears that the motifs (styles) may have been transmitted intact from individual to individual – precisely the type of behavioral *form* transmission that is a prerequisite for cumulative culture (Tennie et al. 2009, Tennie et al. 2012, Dean et al. 2012).

It is worth considering whether our current models of human cumulative culture are too linear for their own good. There is an implicit assumption of progress behind models of human cumulative culture that suggest that different features of this phenomena appeared in a step-wise pattern eventually leading to the modern form of cumulative culture which includes hyper-prosociality and linguistically mediated social transmission largely through pedagogical processes (Hill et al. 2009). The evolution of high-fidelity transmission and cumulative culture may have been marked by fits and starts rather than gradual but constant progress (e.g., McBrearty and Brooks 2000; Isaac et al. 1972). It is possible that the specific adaptations for human cumulative culture (especially motivation and skill in complex forms of teaching and imitating; Tomasello 1999; Tennie et al. 2009; Tennie et al. 2012) existed for hundreds of thousands of years before the appearance of the suite of conditions that are favorable for cumulative culture. That is to say, it remains true for early hominins (and perhaps even for modern day great apes) that – perhaps – the general ability for cumulative culture was and is present, but that it was/is rarely or never expressed. This may be because the actual expression of cumulative culture may depend on factors like rates of environmental change that favor certain amounts of increased social learning and inhibit individual learning (Richerson and Boyd 2005), upright posture (Hill et al. 2009), effective population sizes (Henrich 2004; Kline and Boyd 2010; Powell et al. 2009) and potentially many other factors. Thus, before high-fidelity mechanisms of social learning became regular parts of the human condition, processes associated with low-fidelity social learning and latent solutions for specific tasks may provide more parsimonious explanations of the spatial and temporal variation we see in stone tool assemblages. It is also possible that our ability to recognize cultural transmission in the Early Stone Age archaeological record is biased by the types of artefacts available to us. Would there be little doubt over whether Oldowan hominins had high-fidelity cultural transmission if only we had a record of variation in their hairstyles or digging stick handle engravings instead of stone tool forms?

We find the hypothesis that many Early Stone Age behaviors may have been latent solutions compatible with the available archaeological and comparative psychological evidence. This calls for taking a fresh look at the Early Stone Age record with an eye toward identifying those characteristics that signal the presence of high-fidelity cultural transmission. Rather than assuming that Early Stone Age hominins possessed the same kinds of social learning mechanisms that we possess today, we may be better served by starting with the "null" working hypothesis that they lacked them (informed by what we currently know about great apes) and then modify our working hypothesis as the data warrants.

We find the ZLS hypothesis compelling, but to test it will require identifying features of the Early Stone Age record that could potentially falsify it. Demonstrating that Oldowan or Acheulean tools represent behaviors that are too complex to be learned by a naïve individual (of a tool using species of its time!) would falsify the hypothesis. However, this determination is difficult to make given that Early Stone Age hominins are no longer around and that modern humans may be invalid substitutes because we lack their goals, motivations, build, genetic background, etc.[4]. Relatively little guidance or channeling of the right kind may be all that is needed to ensure the similar outcomes in the case of relatively simple stone tool technologies. For example, simply directing an individual to produce a form that will be an efficient source of flakes or a maintainable edge while keeping a usable grip at the base may be sufficient to (re-)produce a "handaxe" form.

It is worth noting that enculturated bonobos produce and use (crude) stone tools with only little human scaffolding (Toth et al. 1993; and later follow-up studies, such as Roffman et al. 2012) – and considering the tool use proclivities of wild chimpanzees it is at least possible that chimpanzees (perhaps in contrast to bonobos) could learn to make stone tools without any such behavioral scaffolding (experiments that test this hypothesis are currently needed, see also Whiten et al. 2009b). Interestingly, recent nut-cracking studies in chimpanzees established that unintentionally manufactured simple potential stone tools (as by-products of nut-cracking) merely depend on the presence of the right raw material stone types (Mercader et al. 2002). Although the chimpanzees never actually recognized these chips of stone as suitable tools, this may be due to the lack of a need for them. Provided a suitable problem space (as in Toth et al. 1993) or a different ecological niche that involved smaller teeth, longer and more mobile thumbs, and increased consumption of tough animal foods, even the modern chimpanzee mind may indeed be capable of using (if not also intentionally producing) such stone tools. Comparative behavioural studies like these with living great apes show that there is at least the possibility that primitive stone tool manufacture was within the capabilities of the common ancestor of humans and chimpanzees – and thus within the capabilities of Early Stone Age hominins as well. Even if handaxe manufacture is far more complex than the behaviors exhibited by other animals (e.g., weaver birds; Walsh et al. 2010) – and it is not entirely clear that this is the case - this alone is insufficient evidence for the presence of high-fidelity cultural transmission. When we consider early stone tool technologies

[4] And yet, we cannot help but wonder what artefacts would look like if naive modern humans were to be told to produce stone tools that allow the most effective sequential removal of successive flakes ("thrifty stone tools"). Might we expect even modern humans (given enough practice) to come up with artefact forms that might very well resemble handaxes? If the "handaxes as efficient sources of usuable flakes" hypothesis is correct (Ludwig and Harris 1998), this would then explain the form of handaxes (and it would show that handaxes were not only a latent solution at their time, but remain so today). This experiment is unfortunately difficult to do, for various reasons.

within the wider context of animal behavior, it is clear that what we perceive as “complex” does not serve as a reliable diagnostic of a behavior that requires cultural transmission. Complex tools are not necessarily the products of cumulative culture.

And yet, after all of this, it could be that Early Stone Age stone tool technology did in fact require the kinds of high-fidelity social learning mechanisms similar to those observed in modern humans. But it would be necessary to demonstrate this rather than to simply presume it. Indeed, some have suggested that the production process of Acheulean implements would require pedagogical techniques that relied upon the capacity for language (Goren-Inbar 2011). For others, the frequent occurrence of large quantities of handaxes found together at archaeological localities suggests that the implements were produced in a social context (Lycett and Gowlett 2008). But unless a social context necessarily translates into high-fidelity cultural transmission (which, given the evidence from chimpanzees, we doubt), the clustering of tools on the landscape may actually tell us very little about the type of social learning mechanism involved in their production.

In sum, the patterns of variation observed in the Early Stone Age archaeological record are, at the very least, as consistent with a ZLS explanation as they are with models that invoke high-fidelity cultural transmission between individuals. As a consequence, Oldowan and Acheulean stone tools may represent culture (or tradition, sensu Galef 2001), but not cumulative culture. If this proposition withstands future testing, we will need to reconsider the notion that the origin of high-fidelity cultural transmission just happens to coincide with the earliest archaeological assemblages of stone tools. At that point, we may wish to rethink where we place the origin of cumulative culture on the human lineage. Perhaps it makes sense to move it from millions of years ago to hundreds of thousands or even tens of thousands of years ago. What is clear at this point is that much more work is needed to clarify when, why, and how cumulative culture evolved in the Paleolithic.

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